THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SIXTH SERIES.]

No. 116. AUGUST 1897.

XI.—*Notes, Morphological and Systematic, on the Madreporarian Subfamily* Montiporinæ (Montipora *and* Anacropora), *with an Account of the Phylogeny of the* Madreporidæ. By H. M. Bernard, M.A. Cantab.

[Plate II.]

In continuation of the work of cataloguing the National Collection of Corals, I have devoted nearly two years to the study of the genus *Montipora*. I propose in this paper to give a short summary of the morphological results arrived at. Before doing so, however, I should like to take this opportunity of expressing my gratitude to the Director, Sir William Flower, F.R.S., for the friendly interest he has taken in the progress of the work, and also to my friend Prof. F. Jeffrey Bell, who has charge of the coral collection, not only for valuable advice and criticism, but also for much active and willing help.

The first volume of the official catalogue dealt with the genus *Madrepora*, and was written by the late George Brook; the second volume, containing two smaller genera—*Turbinaria* and *Astræopora*—is the work of the present writer. The morphological results arrived at during the preparation of that volume will be found in its introductory chapters and in two papers in this Magazine *. The present study of the Montiporinæ, which, with *Madrepora*, *Turbinaria*, and

* Vol. xv. 1895, p. 499, and vol. xvi. p. 273.

Astræopora, form the family Madreporidæ, enables me to summarize the conclusions arrived at as to the inter-relationships of these genera. That summary will constitute the concluding part of this paper.

The Genus Montipora.

This genus differs in many remarkable points from either *Madrepora*, *Turbinaria*, or *Astræopora*, and doubts as to its affinities are, as we shall see, very prominent in the works of former students. Though founded by Quoy and Gaimard, the name appeared first in print in de Blainville's 'Dictionnaire des Sciences naturelles,' t. lx. (1830), the author having seen it in MS. He placed the new genus between *Gemmipora* (= *Turbinaria*) and *Madrepora* and among a number of other genera, including *Porites*.

In 1834 Ehrenberg* suppressed the genus, distributing the species among the *Porites*. Dana, in 1848, re-established and greatly enlarged the genus, but changed its name to *Manopora*. He objected that the word *Montipora* referred to the cœnenchymatous elevations of the surface, which were not universally present. He thought that the genus *Manopora* was closely allied to *Madrepora*, and, in fact, could be deduced from it by the degeneration of the protuberant calicles.

In 1849 Milne-Edwards and Haime removed it from the Madreporidæ and placed it among the Poritidæ, and to this arrangement they kept in their monograph of the Poritidæ in 1851†; they there noted, however, that *Montipora* showed certain structural resemblances ("quelques rapports de forme") with the Madrepores.

Prof. Verrill at first adopted Milne-Edwards's arrangement, but eventually followed Dana in placing the genus among the Madreporidæ.

Brüggemann apparently came to no conclusion. In two papers which appeared after his death the genus is variously placed. In one the Montiporidæ followed the Madreporidæ and Poritidæ; in the other *Montipora* occurs with *Porites*, *Turbinaria*, &c. under the Madreporidæ.

Prof. Studer, in 1878, followed Milne-Edwards, but in 1880 adopted Dana's classification so far as to class *Montipora* with *Madrepora*. Klunzinger also follows Dana in this respect.

* 'Corallenthiere des rothen Meeres.'

† Ann. d. Sci. Nat. ser. 3, xvi. p. 21.

In 1884 Ridley * denied the close relationship between *Montipora* and *Madrepora* claimed by Dana. The forms of the latter which, owing to the obscuration of the apical polyp, Dana thought might constitute a connecting-link between the two, lent, according to Ridley, no support to such a conclusion, inasmuch as the apical polyps in these types are not really absent, but only inconspicuous owing to their multiplication. Further, it was claimed that a far-reaching difference in the method of budding separated the two. In *Madrepora* the budding is said to be centrifugal, the fresh buds forming below the central apical polyp, while in *Montipora* undifferentiated cœnenchyma takes the lead and the fresh polyps appear above one another. I shall endeavour to estimate later on to what extent this is a true diagnosis of *the* morphological difference between *Madrepora* and *Montipora*.

Duncan, in 1884 †, in his revision of the Milne-Edwards and Haime system, followed these authors in placing *Montipora* with *Porites*.

Quelch, in 1886, in his description of the 'Challenger' Reef Corals, placed *Montipora* among Madreporidæ, as does Miss Ogilvie in her recent "Microscopic and Systematic Study of Madreporarian Types of Corals" ‡.

Lastly, in 1889 Dr. Ortmann §, after following Dana in 1888, classed the Montiporidæ with the Madreporidæ, Poritidæ, Turbinariidæ, &c. as independent families of the Madreporacea.

The conclusion here arrived at on this point, viz. that the *Montipora* belong unmistakably to the Madreporidæ, is based upon a study and comparison of nearly 400 specimens, divisible into some 120 types, of which more than half are new.

The youngest colony that I found is contained in a small oval epithecal saucer, 3·5 millim. long diameter (Pl. II. figs. 1, 2). This saucer is filled with a spongy cœnenchyma. One polyp, about ·25 millim. in diameter, opens in the highest part of the cœnenchyma and near the centre, while a few smaller ones open between it and the epitheca. It seems to me that there is no escape from the conclusion that this largest and most central polyp is the parent polyp of the colony, and that the cœnenchyma stretching from it to the epitheca in which the other polyps open is, or more correctly *was*, before the other polyps appeared, its thick porous wall.

* Ann. & Mag. Nat. Hist. (5) xiii. p. 284.
† Journ. Linn. Soc. vol. xviii.
‡ Phil. Trans. vol. clxxxvii. (1896).
§ Zool. Jahrb. vols. iii. and iv. (syst.).

It will, perhaps, be remembered that I found just such a young colony of *Astræopora*, and, further, I concluded that the morphological differences between *Turbinaria* and *Madrepora* could be best explained by postulating such a young colony in each case; in *Madrepora* the central polyp grew up with tiers of daughters springing from its side, while in *Turbinaria* the ring of daughters shot ahead and formed a cup.

We are then, I think, justified in deducing *Montipora* from a parent polyp opening in a mass of spongy cœnenchyma, *i. e.* with a very thick porous wall, contained in a saucer-like epitheca. In *Montipora*, unlike the Madreporidæ just mentioned, the parent polyp formed no projecting cone, but opened level with the upper flattened surface of its thick wall. Similarly the young polyps, opening laterally, do not form protuberant cones; they appear as mere openings in the cœnenchyma, often in contact with the epitheca, in which case the latter may form part of their outer walls.

The cœnenchyma in the young specimen actually examined consists, as seen from the surface, of jagged flakes, which may be twisted in all directions, but which tend to lie horizontally; the apertures of the polyp-cavities are bounded by the edges of two or more such flakes: in this particular instance the cœnenchyma has been secondarily specialized. From the edges of the flakes points project into the polyp-cavity and form vertical series of spines. These series of spines are, in many types, the only remains of the septal apparatus. Examination of all the types, however, shows that the septa were originally lamellate, as in the other Madreporidæ. The large directives are often continuously laminate, and here and there some of the other primaries also; while, again, what appear to be traces of laminate costæ can be found in the cœnenchyma of very many types. To these important points, as also to the cause of the widespread degeneration of the septal apparatus, we shall return.

Starting, then, from such a young colony, with its parent polyp surrounded by a ring of daughters all immersed in a mass of spongy reticulum contained in an epithecal saucer, the stock may develop along different lines. But while in the other Madreporidæ the *calicles lead and the cœnenchyma fills up the interstices*, in *Montipora* the *cœnenchyma takes the lead* in the formation of the corallum. I am aware that these expressions may, at first sight, appear very loose; they are, however, sufficiently useful to render their employment justifiable, provided we are quite clear as to what they really mean. We must clearly recognize that the

term cœnenchyma applies, in the Madreporidæ, to the fused porous walls of the individual polyps forming the colony. In using the expressions "the calicles lead" and "the cœnenchyma fills up the interstices," what is really meant is that the walls of the individual polyps are distinguishable as such above the level of fusion; where the walls fuse together to form the cœnenchyma they cease to be distinguishable. While, then, in the other Madreporidæ the walls of individual polyps are typically recognizable in so far as they keep above the level of their fusion, in the genus *Montipora* as soon as the parent polyp has budded to form a colony, no matter how small, we can no longer speak of any porous walls except theoretically, for, fusing right up to the level of their apertures, they together form an expanding mass of cœnenchyma. It was this last-mentioned fact that struck Ridley as presenting such a contrast to the method of growth in *Madrepora*; but the true explanation of the difference is not to be found in his "centrifugal" and "centripetal" methods of budding, for it is obvious that any generalization affecting a genus which leaves all the more primitive explanate growths out of the reckoning must be unreliable. The true significance of these comparisons will be still further discussed in the section on the affinities of the genus, as will also the fact that the cœnenchymatous edge of the rim of the cup in *Turbinaria* is closely comparable with the cœnenchymatous edge of a foliate Montipore.

In view, then, of this great development of the cœnenchyma and of its prime importance in building up the Montiporan coralla, we have, it seems, no choice but to utilize the variations presented by the cœnenchyma as the basis of our classification. In so doing we emphasize the fact that the *Montiporæ* are cœnenchymatous corals *par excellence*, that, whereas the cœnenchyma of the Madreporidæ is primarily merely the tissue arising by the more or less limited fusion of the porous walls of adjoining polyps to form a mutual support, in *Montipora* it is more than this. Resulting from the complete fusion of the walls, it has in many cases taken on other functions as well as that of a supporting and cementing tissue, for, rising above the level of the polyp-cavities, it is specialized in various ways for their protection.

A study of the variations which the cœnenchyma presents supports this assumption of its taxonomic importance. The specimens admit of being divided in the most natural way according to the specialization of the cœnenchyma. We also have the additional satisfaction of finding that transition forms reveal the lines along which the leading specializations

have travelled. Hence, although one would never have selected a tissue like the cœnenchyma, which all experience shows to be dangerously variable, as a basis for classification, there is in the present case really no choice, *i. e.* if our morphological diagnosis is correct. Hitherto the variations of the surface cœnenchyma—very superficially handled—have been accorded only a secondary place. Dana, deducing *Montipora* (*Manopora*) from *Madrepora* by the degeneration of the calicles, classified its species accordingly into those in which the protuberant calicles persisted and those in which they had quite disappeared, the latter group being further subdivided according to the form of the corallum and the character of the surface. Milne-Edwards and Haime divided the *Montiporæ* primarily according to the form of the corallum. We may at once dismiss this latter classification as purely artificial. Returning, however, to Dana, it must be noted that there is no evidence whatever to make us believe that *Montipora* is deducible from *Madrepora* by gradual degeneration of protuberant calicles. The only Montiporan forms which Dana adduced as transitional hardly support his contention: one—*M. gemmulata*—has been removed by Verrill to the Turbinarians, while the protuberant calicles in the other—*M. caliculata*—are not true calicles in Dana's sense, but a peculiar specialization of the interstitial cœnenchyma which will be referred to again.

We have, then, no choice but to accept the variations in that tissue, the specializations of which are essentially the peculiarity of the genus, as the basis of classification. Beneath all its baffling superficial variations the laws of its growth can be made out and the main lines along which it has diverged can be traced. This serves to divide the genus into groups which have some claim to be natural. Uncertainty, however, comes in when, in further subdividing these groups, we come within range of the superficial variability due to accidents of position and nutrition. It must therefore be at once confessed that many of the assumed specific variations are not to be relied upon. The "species" established are in many cases only descriptions of individual specimens the surface characters of which give no clue as to their affinities with other specimens. Of course in many cases there are other characters sufficiently striking to justify us in confidently claiming new and distinct types.

The following analysis of the development of the cœnenchyma was only very gradually arrived at after studying series of sections revealed by fractured specimens. It will be best understood if we reverse the process of its discovery,

and, assuming our conclusions to be correct, start from the hypothetical parent-polyp of the genus.

This polyp, as we have seen, differed from that of *Madrepora*, *Turbinaria*, and *Astræopora* in that the porous theca did not rise up into a cone, but was low and thick, filling up, but probably not much overtopping, the rim of the epithecal saucer. Primarily the porous walls consisted of radial laminæ joined together by synapticulæ *, so that the cœnenchyma surrounding this parent polyp may be said to radiate outwards towards the edge of the epitheca. When the first ring of buds appeared just within the edge of the epitheca their walls would also radiate outwards, either continuing to be supported by an extension of the primitive epitheca or shooting out freely beyond its edge. From this initial stage in the development of *Montipora* we should expect to find the cœnenchyma consisting of laminate plates standing at right angles to the epitheca and radiating outwards on all sides. We should expect to find this because the cœnenchyma is nothing but the resultant of fusion of the porous walls of the component polyps, and their laminate costæ would necessarily be arranged in the manner described.

Now this initial stage in the growth of the Montiporan corallum is traceable in almost every type. A surface of fracture through any explanate Montiporan will almost invariably reveal a thin basal layer streaming outwards towards the growing edge. While this basal "streaming layer" is of fairly uniform thickness and the direction of its fibres is always outwards—*i. e.* in the line of growth—its texture may vary. (1) It may be composed of ribbon-like bands running outwards more or less at right angles to the epitheca, but so united as to form a system of flat canals apparently freely communicating with one another. This laminate reticulum, occurring as it invariably does in the "streaming layer," may, I think, safely be regarded as a vestige of the primitive laminate costæ which were once the most important element in the calicle walls. (2) The primitive band-reticulum may, owing to the extensive perforation of the laminæ, have lost this character and have become a filamentous reticulum. In this case also the direction of the threads is typically very pronounced, streaming outwards towards the growing edge. There are, lastly, a few cases in which the reticulum shows no special streaming; these would appear to have been secondarily modified. Here it should be remarked that only

* I use this term generally for all outgrowths from the faces of septa for their mutual support, irrespective of their form and position.

fractures in the direction of growth at any time show the appearance here called streaming; all sections across the streaming show what might be called, in contradistinction, a "stationary" reticulum.

In the figures 3 and 4 *d* (Pl. II.) the artist—Mr. Percy Highly—has well shown by dots the usual appearance of the streaming layer. If these dots are thought of as pores in radial (septo-costal) plates lying in the plane of the paper, the reader will get a fair idea of what I believe to have been the origin of the streaming layer. The relative thickness of the streaming and of the thickening layer in figs. 3 *a*, 3 *b*, 3 *c* should be reversed. The thinness of the streaming layer is probably indicative of the very early budding of the polyps.

We have, then, in all Montiporans (with a few secondary modifications) a basal layer of reticulum streaming outwards (no matter how large or small the colony may be) and forming the growing edge, with or without the supporting epitheca. This streaming layer, which expands the corallum, for some reason or other cannot, as such, thicken it, and the new formation of cœnenchyma for this purpose is in most cases sharply marked off from the streaming layer. An explanation of this thickening layer, shown in figures 3 *a*, 3 *b*, 3 *c*, as compared with 4 *d*, will be suggested later on.

The thickening layer, wherever the epitheca accompanies the growing edge, is confined to the upper surface; but if the growing edge is free, thickening layers may be added to both upper and under surfaces. These layers are derived from the threads or jagged edges of the surfaces of the streaming layer. On the upper surface they grow upwards at right angles to the direction of the streaming, and, uniting among themselves, form a filamentous reticulum. Similarly a layer of reticulum developed from points of the streaming layer bent down at right angles to that layer may cover the under surface. Whereas the upper layer may develop to almost any thickness and give rise to a very great variety of beautiful surfaces, the lower layer seldom thickens much; the individual threads soon tend to thicken, and thus to form a very dense reticulum, and sooner or later the epitheca grows out, covering over the calicles and leading to the more or less complete solidification of the lower surface.

This description of the thickening and solidification of the lower surface does not apply to erect leaves or to branches which may be regarded as thick rounded leaves. In these cases the thickening layer may develop evenly on both sides of the leaf or all round the branches, and show all the surface specializations which in the horizontally growing specimens

are confined to the upper surface. In the case of the branched specimens the tips of the branches which correspond with the growing edge of the explanate forms consist entirely of the streaming layer, and this may be seen forming the axis of all the stems. The cortical layer, which gradually thickens the branches, can in most cases be seen to be formed of threads bending outwards at right angles to the direction of the axial streaming layer.

Leaving, then, the primitive basal streaming layer, we have to consider the variations presented by the upper thickening layer just described :—

(1) It may merely thicken the streaming layer gradually as a filamentous reticulum, the surface in which the calicles open remaining all the time smooth. In reference to the level surface, I have called this group "glabrous," and under it I have arranged some thirty different types (fig. 3 *a*).

(2) The thickening reticulum may grow faster than the calicles, causing the interstices to swell up into ramparts surrounding pits, in the bases of which the calicles open. I have called this the "foveolate" group, after the most extreme type, *M. foveolata* of Dana.

Between these two come specimens which are foveolate while in rapid growth, but eventually become smooth ; these I have called "glabro-foveolate." I have found some twelve foveolate types and five glabro-foveolate.

One specialization of these ramparts has a curious resemblance to true protuberant calicles. This appears to have misled Dana in his ascription of true calicles to *M. caliculata*.

(3) The thickening reticulum shoots up into papillæ which rise up above the general surface. There are several more or less distinct variations of the "papillate" specialization, which at the moment of writing is shown by at least thirty-three types (fig. 3 *b*).

The leading differences are as follows :—(*a*) reticular uprisings froth up the interstices over irregular patches of different sizes ; (*b*) the papillæ are always in some relation to calicles, forming hoods or mounds, on the outer faces of which calicles open ; (*c*) the papillæ run together to form either nearly parallel series in the direction of growth, or else more or less gyrating ridges ; (*d*) lastly, as the extreme type, the papillæ rise as nipple- or nearly symmetrically dome-shaped processes scattered more or less thickly over the surface, but not arranged in radial series (fig. 3 *b*).

(4) The thickening reticulum undergoes a change in its texture ; the threads which bend up vertically become differentiated from the rest of the elements of the reticulum and

become stout solid trabeculæ. The rest of the reticulum merely forms the cross pieces which support these trabeculæ. Every stage in the gradual differentiation of these trabeculæ can be traced. In many cases the more vertical elements of the thickening reticulum run in nearly straight lines, but without thickening. Comparison of specimens shows that the thickening was due to the rising up of the tips of these vertical threads above the surface, perhaps at first as echinulæ. These became stouter and stronger, probably for protective purposes, and thus, as they sank beneath the rising surface, became thick trabeculæ (fig. 3 *c*).

This group, showing the rising of stout trabeculæ above the surface to form protective "tubercles," is very large and contains more than forty types. The distribution and shapes of the tubercles are very varied: they may be densely crowded as minute rounded granules or tall and lancet-shaped; they may be grouped in rings round calicles, or, again, they may run together to form thin keels or ridges. This group is called the "tuberculate" group.

We thus have four main divisions of the genus—glabrous, foveolate, papillate, and tuberculate—each term having reference solely to a peculiar specialization of the cœnenchyma. While the first three of these terms need no comment, the last requires justification.

In all the earlier descriptions of Montiporan types the terms papillæ and tubercle seem to have been used indiscriminately. It is often impossible to tell whether a writer was describing a specimen belonging to group 3 or to group 4. The most important use of the word tubercle occurs in Lamarck's description of the specimen *Porites tuberculosa*, Lk. (=*Montipora tuberculosa*). In fixing the use of the word tubercles to mean the small solid tips of individual trabeculæ when they project above the surface, I have been led to do so by the conviction that these were Lamarck's "tubercles" as seen on his type "*tuberculosa*." Certain expressions in Lamarck's text point clearly to this. In describing *P. tuberculosa* * he speaks of "les tubercules dont la surface est parsemée" as being "graniformes ou columniformes;" and, again, on the next page he speaks of interstices being "hérissés de tubercules." Both these expressions are quite inapplicable to the much larger swollen reticular knobs here called papillæ.

One other remark on these tubercles with their trabecula-like sunken portions. It was the presence of these trabeculæ which appears to have misled Milne-Edwards. He compared

* 'Animaux sans Vertèbres,' ii. 1816, p. 272.

them with the entirely different trabeculæ of *Porites*, and accordingly placed *Montipora* among the Poritidæ. So far as my own observation goes, the two are morphologically distinct; the trabeculæ in *Porites* are primitive structures, rising straight up from the epitheca, while in *Montipora* they are, as we have seen, quite secondary.

Turning from the cœnenchyma to the polyps, polyp-cavities, method of budding, and to the forms of the corallum, points which are, as a rule, of prime importance, we find that the special development of the cœnenchyma has, as it were, overshadowed them. With regard to the last-named, we find all the typical methods of growth in each of the four chief divisions based upon the specializations of the cœnenchyma. The polyps themselves are minute and their tentacles are little more than papillæ or crenulations of the edge of the oral disk. The polyp-cavities are also very small and the septal apparatus as a rule degenerated into mere vertical rows of projecting spines. The largest or directive septum with a few of the larger primaries may be more or less interruptedly laminate. I look upon these as survivals of a primitive laminate condition of the septa and costæ in the thick porous walls. The cause of this degeneration of polyps and septal apparatus may perhaps be correlated with the great development of the cœnenchyma, the production of which must be a strain on the resources of the living organism, leading to the fixation of the polyp at a very undeveloped stage. In contradistinction to this extreme we may cite in support of our suggestion the cases of the *Alcyonaria* and *Actinia*, in which the polyps reach a very high level of development, while the skeletal matter deposited is either scanty or altogether absent.

The character of the budding, as also a few further points on the degeneration of the septal apparatus, will be referred to in the concluding section on the interrelationships of the Madreporidæ. In that connexion such matters can be more advantageously discussed comparatively. We shall there also summarize the description of the genus above given, and in that way emphasize the arguments in favour of classing *Montipora* with the Madreporidæ.

The Genus Anacropora.

This genus, founded by Ridley in 1884 (*l. c.*) to contain a branched coral from Keeling Island, was said to be distinguished from *Madrepora* by the method of budding and from *Montipora* by its protuberant calicles.

The method of budding in *Madrepora*, in which smaller

daughters appear from the sides of larger parent ("apical") polyps, was described as centrifugal, while that in *Anacropora*, in which an apex of undifferentiated cœnenchyma takes the lead and the young polyps appear in it as it grows, was called centripetal. The distinction was thought to be fundamental. On the other hand, the new genus came very near *Montipora*, differing from it chiefly in the fact that the calicles in *Montipora* are typically immersed, while in *Anacropora* they bulge up the surfaces of the branches into mounds or eminences.

The new genus was accepted at once by Duncan in his revision of Milne-Edwards and Haime's system, and he allied it with *Montipora*.

The 'Challenger' expedition brought home two new types, which Quelch classed under Ridley's genus, and in 1892 Rehberg * added another specimen and type, bringing the number up to four. The following notes are based upon the study of the specimens and fragments (twenty-two in all) in the National Collection. These include all the existing types except that of Rehberg (*A. spinosa*), which is in the Hamburg Museum. The examination has resulted in the establishment of two new types, one being represented only by fragments, the bulk of the specimens being in the Vienna Museum. Full details will appear in the official catalogue, which is in the press.

I was for some time quite uncertain as to the validity of the distinction made by Ridley between *Anacropora* and *Montipora*. Slight mounds or elevations on which the calicles opened might and do, indeed, occur in *Montipora*, wherever the corallum is very thin, while, on the other hand, we have in *Anacropora* the streaming axial layer leading the growth, and forming, as in *Montipora*, the tips of branches, and a further cortical layer formed just as in *Montipora*. It seemed to me, therefore, that while the fundamental identity in the structure of the colonial skeleton showed that *Anacroporæ* were really Montipores, the presence of protuberant calicles, which might be a slight return to primitive conditions, hardly justified the establishing of a new genus. Comparison with other types and with the undescribed material in the collection has, however, revealed other characters which are important enough to warrant our retaining the genus, but uniting it with *Montipora* under a subfamily Montiporinæ.

While, then, the fundamental identity in the structure of the cœnenchyma shows that *Anacropora* has branched off

* Abh. Nat. Ver. Hamb. xii. p. 46.

from *Montipora*, we may assume that the protuberant calicles, which may, in some cases, be even tall and conical, suggest that this branching off took place at a very early stage in the development of that genus. That these protuberances are primitive, and not secondary returns to primitive conditions, may, perhaps, be gathered from the very important fact that the primary septa in the more protuberant calicles are laminate, and, further, that these laminate radial structures may even project down the outer wall of the protuberance as costal ridges (Pl. II. fig. 5). It is specially worthy of note that the less protuberant calicles, or those which open flush with the surface, have the degenerated septal apparatus characteristic of *Montipora*, while those which grow taller and slightly larger develop radial skeletal laminæ, septa and costæ. While it is of course quite possible that this is a secondary return to primitive conditions, there is no reason why we should not assume it to be the persistence of such conditions. The burden of proof, I think, rests with those who prefer the former suggestion.

I have been much struck by noting that many of the protuberant calicles with costal ridges running down their sides show the tendency to a spiral twisting of the whole calicle which I have already referred to in *Turbinaria* and *Madrepora*. This fact, again, seems to me to suggest that the protuberance of the calicles is primitive and not atavistic.

Hence, then, we conclude that *Anacropora* branched off from *Montipora* before the degeneration of the calicles and of their laminate radial skeleton had gone as far as it now has in the latter genus.

In this connexion it is worth noting that the axial streaming layer is typically laminate or band-like, and that, in those cases in which it appears most filamentous, examination shows that this is a secondary condition due to the formation of large perforations in the primitive longitudinal bands. This band-reticulum, as we have seen above, can be best traced to the outward streaming of the primitive laminate radial structures composing the chief portion of the thick walls of the parent and daughter polyps in the earlier stages of colony formation.

In addition to this important laminate structure of the walls of the more protuberant calicles, the method of branching is quite peculiar. All the known types are composed of rather thin cylindrical stems more or less knotted (by the protuberant calicles) like a thorn-stick. While the stems are generally slightly curved, the branches come off suddenly at rather wide angles, the stem at the same time bending

away from the branch. It is, in reality, a kind of forking, only the stem remains the more important and less diverging prong. The result of repeated branchings with free fusions between parts that touch is to form a rather closely matted tangle low down near the ground, the meshes in the tangle being more or less angular. This angular character of the meshes is, however, frequently obscured by curvings of the branches. Broken fragments falling down into the tangle freely fuse on again, and help to make the net thicker. In claiming this very peculiar method of growth as characteristic of the genus I am aware that it is not immediately evident in all the types. It is very marked in Ridley's original type (*A. Forbesi*), in Quelch's types (*A. gracilis* and *A. solida*), and in one of the new types (*A. echinulata* *), whereas it is not so marked though traceable in *A. erecta* *, and apparently least visible in Rehberg's type (*A. spinosa*). In these last two forms the branching does not come off at such a wide angle, and hence the whole corallum is more symmetrically arborescent. But in *A. erecta*, so far as I remember the photographs shown me by Dr. Marenzeller, the larger clumps were very close tangles of thin knotted stems, and Rehberg's figure of *A. spinosa* (*l. c.*) appears to show distinct traces of a tendency to sudden angular bendings of the stems and branches.

These points, then, the protuberant calicles, showing distinct lamination of their radial structures, and the peculiar character of the branching, serve, I think, to separate *Anacropora* from *Montipora*, with which genus it is, however, fundamentally associated in the structure of the cœnenchyma and in the presence of calicles with degenerate septal apparatus exactly like those of *Montipora*.

Interrelationships of the Madreporidæ.

As we have above seen, the only argument for allying *Montipora* with *Porites*, as was done by Milne-Edwards and Haime, and later by Duncan, falls to the ground as soon as the secondary character of the trabeculæ is established †. Hence we have no hesitation in claiming the genus with its ally *Anacropora* as together forming a subfamily of the Madreporidæ. I shall now endeavour to show that the remaining three accepted genera—*Madrepora*, *Turbinaria*,

* Full descriptions of these are given in the Museum Catalogue.

† In 1889 Dr. Ortmann suggested, without going into details, that *Montipora* might be deduced from *Porites* through *Alveopora* (Zool. Jahrb. (syst.) iv. p. 584).

and *Astræopora*—can be usefully united in a second subfamily; so that, for the future, the Madreporidæ will consist, so far as we at present know, of two subfamilies—the Madreporinæ, comprising three genera, and the Montiporinæ, comprising two genera.

The strongest argument in favour of this classification lies in the fact that the five genera can be deduced from a common ancestral form. In describing this form we are, for obvious reasons, confined to a consideration of its parent polyp, and not of its colony. Every colony starts from a parent polyp, and, indeed, receives its chief characteristic from the structure, growth, and method of budding of this individual, directly developed from the attached larva. Hence it is enough if we can trace any group of colony formations back to a common ancestral parent polyp.

Reference to the analyses already given in this and in the earlier papers on *Turbinaria* and *Astræopora* shows that this common parent polyp possessed the following leading characteristics:—(1) a porous wall, with laminate radial structures; (2) a well-developed saucer-shaped epitheca; (3) the habit of very early budding while the parent polyp was still very small; (4) the production of true buds, starting from the smallest beginnings out of the sides of the polyp, and forming their skeletons, at least in the first stages, upon and with some slight modification of the radial symmetry of the porous wall of the parent polyp*.

From such a form we may deduce the genera under discussion along the following lines of specialization:—

Madrepora.—The skeleton of the parent polyp grew in height, and consequently somewhat in size, shooting upwards in a tall cone with thickening base (fig. 4*a*). The buds grew out in tiers from its sides, remaining comparatively small. The radial structures persist as laminæ, and those septa of the buds would be largest which could start at once upon, and in the same plane with, one of the radial laminate structures (costæ) of the parent; hence the "directive" septa of the buds are typically radially symmetrical with those of the parent. The epitheca is left behind.

Turbinaria.—A ring of buds shoots up round and from the sides of the parent polyp, together forming a cup, the wall of each bud rising up as a distinct cone above the level of the fusion of their walls to form the common cœnenchyma (fig. 4*b*).

* For Miss Ogilvie's alternative derivation of the Madreporidæ see Phil. Trans. vol. clxxxvii., 1896. This has been criticized by me in the Geological Mag. vol. iv. 1897, p. 170.

The parent polyp dies away, and its primitive protuberant cone is immersed under the cœnenchyma formed from the fusion of the walls of a ring of daughters. These daughters carry on the colony, the budding of the daughters being limited to their free or outer sides, *i. e.* to the sides turned away from the axis of the cup. Hence the fact referred to above, that in *Turbinaria* as well as in *Montipora* the young buds appear in the undifferentiated cœnenchyma which forms the growing edge of the cup. This edge represents morphologically the outer sides of the combined porous walls of the last-formed ring of polyps, and differs from the porous wall of the parent polyp mainly in the facts, (1) that the laminate radial structures are more or less obscured, and (2) that the epitheca has been left behind. The polyps forming the Turbinarian colony develop equally, and there is no such disparity in size as is seen between the axial polyp of *Madrepora* and its daughters. Principal or directive septa occur and can be accounted for in the same way as in *Madrepora*.

Astræopora.—The budding is promiscuous; a new bud develops wherever there is room for it, each one typically carrying up its wall into a protuberant cone (fig. 4 *c*). As a result of this crowding the known forms are, without exception, thick encrusting, or massive. The costal radial structures of the original parent ceased to be laminate, but broke up into radial series of spines, the tips of which formed protective echinulæ. One apparently natural consequence of this was a considerable degeneration of the septal apparatus in the daughters of the colony.

Montiporinæ.—The original parent polyp was distinguished by great thickness of its porous walls, which apparently early arrested the development of the polyp, and by a tendency of the whole skeleton to be low, and even perhaps disk-like, and not to rise up into a cone as in the last three genera (fig. 4 *d*). In the modern Montipores this has reached its extreme limit, but in *Anacropora* the habit of forming conical walls is not yet lost. The synapticular connexions between the radial structures reached far in towards the centre, so that the visible septal apparatus tended to be limited to rows of septal spines; when the calicles protrude (*Anacropora*), and hence grow a little in size, laminate septa appear. The tendency to enormous thickness of porous wall was inherited by the daughter polyps. Hence the two chief characteristics of the genus—(1) minuteness of the polyp-cavities, (2) great richness of cœnenchyma, which is nothing but the result of fusion of the greatly thickened porous walls of the individuals of the colony. The budding

of the daughters seems, as a rule, to be limited to their free or outer sides; the fresh buds turn upwards if the growing edge is accompanied by an epitheca, but may turn up or down indifferently if the growing edge is free. In the diagrams the former case is, for the sake of simplicity, alone illustrated.

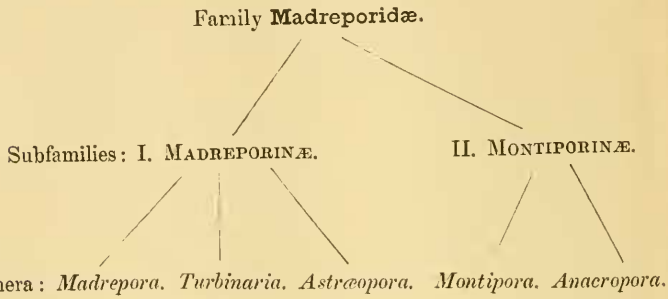
In *Montipora* we have almost all possible growth-formations resulting from this aggregation of small thick-walled polyps, aided by the secondary additions of tissue, above described as the "thickening layers." These begin to form at varying distances from the growing edges or apices, *i. e.* after the budding of the polyps has ceased. May not this fresh growth be correlated with the very early budding of the Montiporan polyps and their subsequent continued but limited growth—limited, that is, by the abundant secretion of skeletal matter—which is the characteristic feature of the genus?

In *Anacropora* the growth-form is highly specialized. We may thus look upon *Anacropora* as a survival of a special growth-form of some more primitive Montipore, *i. e.* of some Montipore in which the degeneration of the protuberant conical wall had not gone so far as it has in the modern representatives of the genus. While in *Montipora* the laminate radial elements of the calyx have almost entirely disappeared, being only occasionally found in a few large primaries, directives and others, and, again, in the streaming layer of the cœnenchyma, in *Anacropora* laminate septa and costæ appear in the more protuberant calicles in addition to the lamination of the streaming axial layer. It is further worth noting that not only does the occasional presence of laminate directives support the deduction of *Montipora* from an ancestral polyp with laminate radial skeleton, but the mere presence of directives points also that way, that is, if the explanation of the rise of directives above given is correct. The primitive epitheca, which is lost in *Anacropora*, persists and plays a great part in the formation of many Montiporan coralla.

In these different ways all the genera which are at present included in the Madreporidæ can be deduced from a common parent. The two last mentioned are associated by the peculiar structure of the cœnenchyma, which, as we have seen, is traceable to the great thickness of the porous walls of the individual polyps. These, then, form the subfamily Montiporinæ. The remaining three genera are also united by one character in common, viz. the typical upgrowth of the polyp-walls into freely protuberant calicles, their basal portions alone being fused together to form a cœnenchyma. I can see no reason why this character should not unite *Madrepora*, *Turbinaria*, and *Astræopora* into a second subfamily—the

Madreporinæ. The chief objection to this rests in the specialized character of the laminate radial structures of *Astræopora*, which ought, perhaps, to separate that genus from *Madrepora* and *Turbinaria*. In the meantime, however, they can be usefully united in the manner suggested.

I therefore suggest the following arrangement of the family :—



A serious objection may be raised to this description of the phylogeny of the Madreporidæ, viz. that it is apparently based exclusively upon study of the five genera dealt with. It is true that such a limitation of one's survey makes all generalizations hazardous. I am, however, encouraged to state the conclusions I have arrived at with regard to these genera even at this early stage because they are not based solely upon study of the five genera concerned. Most of the other Madreporarian genera—at least, the better known of them—have been studied and compared again and again for the express purpose of arriving at some clear insight into the different lines along which the stony corals have been differentiated. I am aware that this does not appear from anything said in this paper. I have, however, here purposely abstained from making any definite morphological statement about any genus which I have not studied systematically. The survey of a few specimens of any particular genus may give reliable hints for guidance towards a better understanding of the genera which are at the time the object of close study, but cannot be exact enough to admit of definite assertion. It is, indeed, quite possible that when all the available specimens of the genus *Porites* have been under review, the purposely very limited reference to the morphology of that genus given above may have to be qualified.

EXPLANATION OF PLATE II.

Figs. 1, 2. Youngest colony of *Montipora* found, 3·5 millim. in long diameter: *pp*, the largest and tallest calicle, presumably that of the parent polyp of the colony. The saucer-shaped epitheca has been turned in, and the outward growth at *a* has been hindered; hence the initial symmetry has been destroyed, the young stock having expanded chiefly in the direction of *b*.

Fig. 3. Diagrams showing the building up of the Montiporan corallum. The budding of the thick-walled polyps is shown by lines: the originally laminate septa and costæ lying in the plane of the paper are covered with curved dotted lines, to represent the ordinary appearance of the basal streaming layer in sections at right angles to the growing edge. The tissue which secondarily thickens the corallum is:—

(*a*) A reticulum which does not rise above the level of the calicles.

(*b*) A reticulum which surges up to form spongy ramparts or papillæ.

(*c*) A reticulum of which the more vertical elements are straightened and thickened and project above the surface as tubercles. In these figures the streaming layer has been drawn very thick for the sake of clearness. In reality the relative thicknesses of the layers should be reversed, the streaming layer being, in many cases at least, the thinner.

Fig. 4. Diagrams to show the different specializations in form and method of budding of the parent polyp, which will explain the leading characters of the four chief Madreporidan genera:—(a) *Madrepora*, (b) *Turbinaria*, (c) *Astræopora*, (d) *Montipora*.

Fig. 5. A protuberant calicle of *Anacropora gracilis* (× ca. 20), showing the laminate septa and the edges of the costæ running down the outer walls.

XII.—*Contributions from the New Mexico Biological Station.* —VI. *The New Mexico Bees of the Genus* Heriades, *and a new* Halictus. By T. D. A. Cockerell.

The bees herein described all fall under *Heriades* in the broad sense, but they present considerable differences, which might be considered of subgeneric or even generic value.

A. *Legs partly red.*

a. Smaller species, the red confined to the front legs.

Heriades asteris, sp. n.

♂. Length about 5 millim.

Black, with the anterior femora in front and within and the broadened anterior tibiæ behind ferruginous. The whole insect very coarsely sculptured, the punctures of the vertex and mesothorax extremely large, producing a subcancellate